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ART. VIII.—*Ecological Studies in Victoria. Part III.—Coastal Sand Dunes.*

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(With Plates VIII. and IX.)

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Coastal Dunes are a universal phenomenon, and, as remarked by Lundegardh (4), they are very similar ecologically, no matter where found, but the species which constitute the vegetative cover, while being morphologically similar, may be entirely different taxonomically.

In all latitudes, the dune plants are subjected to the same environment, but the particular species present is mainly a matter of the floral province in which the dune finds itself. This is well illustrated by the dunes along the Victorian coast, and the majority of plants found are closely related to typical Australian genera and families.

Although we are considering the dune as an association (and indeed Dune Vegetation is of a special type), it must be borne in mind that from the outermost or seawards dune to the innermost, there occurs a succession, both of growth forms and of species, so much so that there is a greater difference between the vegetation of the first and last dune than is usual between many associations, or indeed higher units (Pl. VIII. B, IX. C.) Nevertheless, by common consent, we take the dune vegetation as a unit, since the two main factors of the environment, sand and wind, are the determining factors in fixing the limits of the association. Once the sand is fixed permanently, other associations take the place of the coastal vegetation. Thus we find that both *Eucalyptus viminalis* and its common associate, *Pteridium aquilinum*, are present in the area immediately succeeding where the dunes have been fixed, but they do not occur in the area of moving sand. The dunes then cannot be said to have a uniform physiognomy, nor a constant composition, except spacially. The composition is constant from front to rear, but not in any unit area. If we were to take quadrats, even of very large size, they would give very differing results. Nevertheless, across the width of the dunes the same factors of environment are operating, but their incidence steadily diminishes from front to rear, and at last ceases to have effect. It is a peculiar feature of this association that the environmental factors change comparatively rapidly. As a rule, the environmental factors are uniform throughout an association, but here, as indicated, the uniformity is only in space, and not in minimum area. The definition of Flahault and Schroter (Braun Blanquet (1)) that an association has definite composition, must be read in a very broad sense.

Uniformity there is, however. The recognition of the Dune Vegetation as a unit of Vegetation, and not several units, bears witness to the fact that it is the environment which finally determines the particular association and growth forms found in any particular locality. No one would attempt surely to separate Dune Vegetation into its two extreme constituent parts, Grassland and Forest (Pl. VIII. B, IX. C), which are distinctive enough. There is here from first to last a struggle for existence. The sand dune is in a hostile area (Pl. IX. A), and on the outermost dune the hostile forces of the environment, advancing from the sea, meet the outposts of vegetation advancing from the land. (Pl. IX. B.). The moving sand, derived from the disintegration of rocks by the constant action of the sea, is finally arrested, and the vegetation makes a complete canopy (Pl. VIII. B).

Although we pass from grass to trees in the succession, the change is due to the modification of the unfavorable elements, moving sand and wind, by the vegetation itself. This feature compels one to keep dissimilar elements, grass and trees, together in the one association. In other areas, where trees or shrubs abruptly succeeded grassland (Pl. VIII. C), one would naturally expect a material change in the environment.

Environment is the primary cause of plant associations whose distinctive features are due to the growth forms occurring in them. Hence classification of associations to be truly scientific must ultimately rest on the cause or effect, i.e., on either the environment or growth forms. Linnean species, as such, retreat into the background as a basis of classification. Indeed, it can be shown that Linnean species themselves are partly the outcome of the environment. The members of diverse associations may be related taxonomically, but wholly unrelated ecologically. Thus the dunes along the Victorian coast bear the genera *Helichrysum, Olearia, Senecio, Leptospermum, Acacia,* and *Banksia,* as may the adjacent heath lands, but the two associations are not related ecologically. It merely illustrates the fact that the composition of any particular association is due to the general floral composition of the land in which it finds itself. Thus we shall see that the sand dune flora, which essentially is characteristic, yet is taxonomically connected with other widely differing associations. Change or variation is an inherent quality of life and, through this, forms are evolved which gradually colonize new land areas capable of sustaining plant growth.

The dune, since it is new land, is populated by a pioneer vegetation. This is the same in all climates, and it is of interest to note the families and genera that contribute to these pioneers. It may be concluded, since those families and genera, constituting the settled and stable communities in the hinterland, give rise to the population of the adverse area, that evolution and environment are closely associated. Not all evolution is a response to environment, but the latter is a contributing factor.

In a pioneer vegetation, but few forms are to be found. The limit of variation has to be stretched wide, hence few occur. The more favorable a locality, generally the greater is the number of species. The Fern Gully may be regarded as an exception, but it is an association far removed from its chief source of development. The front rank of the dune association is essentially composed of pioneers, which stand, not in close proximity (Pl. IX. C), but far removed from one another. Conditions of life are hard, and the struggle against the destructive forces of inanimate nature is severe. Struggle for existence goes on in two directions; firstly, against similar individuals, in which thousands perish for each survivor which is more or less perfect; secondly, against the destructive forces of nature. They survive only because they rise superior to their surroundings.

Dunes exist extensively along our coast, but although the same forces are operating, they differ appreciably both as to their degree and extent of development. They may be only a few yards wide or, as at Tarwin Meadows, may be hundreds of yards wide. All stages of development are met; there may be only fragmentary parts of the typical dune vegetation, or there may be complete development, from free sand to complete cover, as at Lakes Entrance. While attention has been given to the dunes at various points along the coast, the occurrences at Lakes Entrance have been most closely studied.

The Habitat.

A. Sand.

Were it not for the constant action of the wind the sand would be very readily settled by vegetation. In the dune the moving sand has to be arrested effectively before satisfactory colonization can finally take place. The sand is composed chiefly of silicon dioxide, but in the vicinity of rocky headlands, as along Phillip Island, where both seaweeds and shell fish are abundant, both the organic and calcareous content may be high and conspicuous to the naked eye. Neither of these constituents, however, affects the vegetation of the dunes. They are broken down into fragments as small as sand, and physically behave as such. In other areas, as along the Ninety Mile beach, both the organic and calcareous content are low. Any chemical or other effect that such constituents might have in other associations is lost here, since the physical environment is of greater consequence. Evenness of size of particle is an outstanding character. Darbishire (2) gives the size of grains in the dunes investigated by him as between 0.2 and 0.4 mm., while Warming (10) states that the grains generally average $\frac{1}{3}$ mm. In Table I. is given a series of analyses of material taken from dunes along the Victorian coast, and for comparison analyses of drift sand from the Victorian Mallee and of dune sand collected by the author in the Northern Sahara, in the vicinity of Biskra, Algeria, are included. The sizes of the fractions are given in inches.

TABLE I.—MECHANICAL ANALYSES OF SAND DUNE MATERIAL.

Locality.	Percentage of Fractions—Inch.					
	1/10 to 1/20.	1/20 to 1/40.	1/40 to 1/60.	1/60 to 1/80.	1/80 to 1/100.	Less than 1/100.
Phillip Island ..	..	1·14	**48·50**	46·00	4·20	·04
Tarwin Meadows ..	..	·07	13·25	**60·75**	23·50	2·17
Brighton Beach ..	·05	·11	27·33	**62·66**	8·50	·95
Lakes Entrance ..	..	11·20	**81·01**	7·45	·29	..
Mallee Drift ..	·01	22·20	**50·31**	12·22	5·80	9·41
Sahara	..	·95	21·00	**50·00**	20·00	8·05

It will be noted that a high percentage of the grains lies between 1-40 (0.6 mm. app.) and 1-80 in. (0.3 mm. app.). The lower limit is in agreement with those of Darbishire and Warming. The grains are not strictly spherical, but are more or less ellipsoid or ovoid as indicated by Darbishire (2). The similarity in the size of sand grains constituting dunes in various parts of the world suggests that the forces forming them are similar. It has been found by Vageler (9) that there is a relationship between strength of wind and size of sand particles moved, expressed in the equation

$$y = .0268x,^{1.568}$$

where y = diameter of particle in mm., and x = wind velocity in metres per sec. For a particle 0.5 mm. in diameter, which closely corresponds to 1-50 in., this formula would give a value of 6.46 mm. per sec.. or slightly more than 14 miles per hour. Experiments with the fraction 1-40–1-60 in. showed that the grains just moved in a wind speed of 12 miles per hour, but moved freely at 15 miles per hour, which agrees with the value obtained from the formula. It has been shown by Stevenson and by Hellman, quoted by Lundegardh (4), that wind velocity is greatly retarded by the earth's surface, and that the wind velocity steadily increases upwards. Thus, to quote Lundegardh, the force at 0.05 m. and 0.5 m. is as 1 : 1.9, that is nearly twice as great at half a metre above the surface; a strength, then, which will just move sand, must be blowing in the shrub phase at about 30 miles per hour. A wind with sufficient velocity to move the sand grains only occasionally blows, and therefore sand movement is irregular. It will be found on examination of sections of dunes that they are built up intermittently, and not continuously.

B. MOISTURE.

It would appear from some writers on sand dunes that drought is a feature of the habitat, and that the xeromorphic character of dune vegetation is the outcome of the xerophytic conditions there existing (Schimper (6)). Darbishire (2), on the other hand, quotes Swellengrebel as stating that the lower layers of the dunes are tolerably moist. The moisture content of these layers he believes to be under the influence of the ground water. This may be true for very shallow dunes, but in high dunes, such as occur at Tarwin Meadows, this cannot be so. The roots of *Spinifex hirsutus* have been traced down 6 feet, but ground water is not found at that depth. The dampness of the deeper layers is due entirely to the percolation of rain water. In contrast to other associations, no rain water is lost in run-off, and very little in evaporation, for practically all the rain that falls passes into the soil. Experiments with percolation of water through dune material show that an inch of water penetrates on the average 3.3 inches into the sand, so that a rainfall of 30 inches would sink 8 ft. 3 in. However, the depth to which this amount of water actually penetrates is much greater than this. The depth to which water will percolate is governed not only by the character of the soil particles, but also by the depth of the moist sand itself. When the water has sunk to a certain depth, it exerts a downward pull on the upper portion of the water column, and therefore less water is held in the upper layers of soil than when only a few inches are present. The high percentage in the upper layers of the soil can no longer be held by the sand grains against the force of gravity, and therefore the water-holding capacity of the upper layers varies with the depth to which the moisture has penetrated. The experiment of adding small and large quantities of water to long columns of dune sand, arranged so as to permit of drainage from the bottom, showed that after equal intervals of time the amount of moisture of the upper 2 inches in the short moistened section was always much greater than that of the upper 2 inches of the long moistened column. After standing for 24 hours, it has been found that the ratio of moisture in the short moistened section to that of a similar length from the completely moistened column averaged 5.9 : 1. Furthermore, if a long column be completely saturated, and then left to drain, evaporation from the upper surface being guarded against, there is, as long as the experiment be conducted, a very great difference in the moisture content between the upper and lower portions of the column. This has been extensively studied by King (3).

Size of soil particle and depth to which the moisture penetrates are not the only factors, for time is also a factor in determining the amount of water in the upper layers. Hence the usual determination of water-holding capacity of soils has no real ecological significance. In Table II. are given the moisture contents of the upper 2 inches of sand columns 73 cm. long and 2.3 cm. in diameter, the columns being first saturated, and then left to drain for varying lengths of time, the first measurement being taken after dripping at the bottom had actively ceased.

Table II.—Moisture Content of Upper 2 inches of a Saturated Sand Column Left to Drain for Times Given.

Time.	Percentage of Moisture.
	%
3 hours	5·6
24 hours	3·3
48 hours	3·0
15 days	2·3

The depth of the moisture available for plants in the dunes is thus very variable, depending not only upon the above factors, but also upon the amount of sand that has been added to or removed from the area by the wind. Along the Victorian coast it rarely happens that the plants are in need of water, but in the year 1923 the water content had reached an amount too low for the needs of these plants, and wilting occurred extensively. The rainfall for the six months, November to April, for 1922-23, as well as the average for these months, is given in Table III.

Table III.—Comparison of Average Monthly Rainfall of Melbourne with that of 1922-23.

Month.	Actual Rainfall.	Average 66 Years.
	Points.	Points.
1922—		
November	105	224
December	202	232
1923—		
January	99	188
February	61	170
March	33	223
April	0	223

It has been repeatedly found that the dunes are constantly moist a short distance beneath the surface, and during the early part of 1934 a series of investigations was made to ascertain the moisture content, the results of which are given in Table IV. At Melbourne and Cowes (a few miles from Cape Woolamai), the rainfall for February and March was below normal, and conditions were favorable for a low moisture content of the soil. At Lakes Entrance the rainfall was well above normal. The samples were all taken from the highest point of the dunes; those at Woolamai being taken at an elevation of 100 feet.

TABLE IV.—MOISTURE CONTENT AT VARIOUS DEPTHS OF SAND DUNES.

Locality.	Date.	Moisture Content.					
		Surface.	6 In.	12 In.	18 In.	24 In.	30 In.
Lakes Entrance ..	5.2.34	..	2·06	..	2·85	..	3·12
Brighton Beach ..	14.3.34	Trace	1·06	1·26	..	..	..
Cape Woolamai ..	17.3.34	0·33	1·44	2·23	2·4	..	..
Lakes Entrance ..	2.4.34	..	2·7	..	2·3	..	2·9

The percentage of moisture in the dunes appears to be very low, but germination experiments with wheat and mustard showed that these seeds can germinate in dune sand with as low a moisture content as 1 per cent., and from this it may be assumed that the amounts of moisture given in Table IV. are generally sufficient for the growth of plants.

The rapid entry of rain water and its continuous movement downwards are both important factors in the conservation of moisture, but equally important are the new layers of dry sand blown over the moistened area. Usually wind is a desiccating agent, but on the dune it acts as a conserver of moisture by adding the sand mulch. How effective is the retardation by a dry sand layer of water loss from damp dune sand can be seen from Fig. 1, where the losses from bare surface are contrasted with similar surfaces covered by 1, 2, and 3 cm. of dry sand respectively.

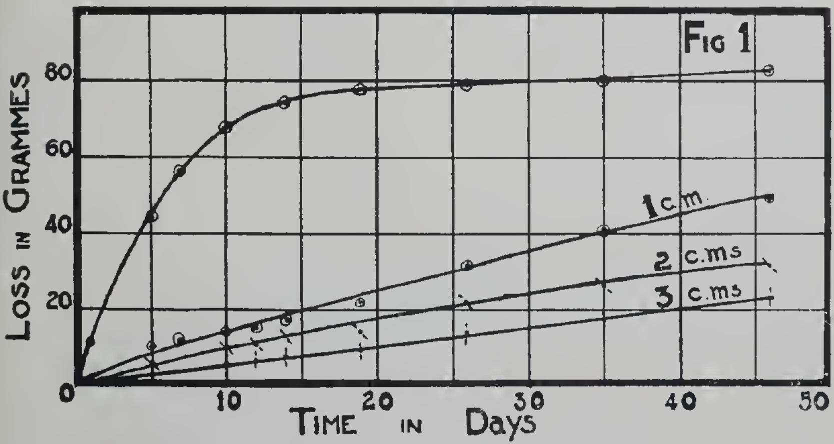


FIG. 1.—Effect of sand mulch on the loss of moisture from moist dune sand.

It is probable that with all the factors operating for the conservation of moisture, the evaporation loss is surprisingly small. This, together with the uniform distribution of rain (Table V.) throughout the year, indicates that there is normally no scarcity of moisture at the roots, and therefore the habitat, in so far as the soil is concerned, is in no way xerophytic.

Table V.—Distribution of Rain Throughout the Year for Stations along the Victorian Coast.

(Rain recorded in points; 100 points = 1 inch.)

Station.	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.	Average Annual.
Portland ..	136	138	163	264	371	412	**422**	417	347	281	194	180	3325
Cowes ..	182	154	251	261	238	**320**	275	287	280	258	220	213	2989
Lakes Entrance	258	174	262	223	217	231	234	181	243	**293**	209	243	2768

Although the dunes are in close proximity to the sea, the salt content of the dune is very low and negligible from an osmotic point of view. The contrary view was held by Schimper (6), but Warming (10) and Darbishire (2) have found the same condition, so that it may be taken as a feature of environment that the water in the sand dune has no osmotically ecological significance. Even if salt were present, its solubility and the ready percolation of water would cause the salt to be carried far down out of the region of the roots.

C. Dune Building.

It is only on the outer dune that sand is free to move. The distance, however, from the high-tide level to the arrest of the sand differs enormously. At Sydenham Inlet, the dunes are densely clothed but a few yards from high tide, while at Tarwin Meadows there are some hundreds of yards between these two points. The reasons for these differences are probably that the amount of material produced is more at some points than at others, and also that the conditions favouring accumulation vary. In this latter connection, land of low elevation extending for a considerable distance inland is more favorable for extensive sand accumulation than where rising ground exists. The narrowness of dunes, on the other hand, may be due to the destructive force of wind, or to the encroachment of the sea upon the land. Dunes are not built continuously and gradually, but rather by layers, since wind action is not constant. In breached dunes the successive layers may be seen. There are two sand-fixing agents, water and plants. Water has a binding action, and holds the dunes against the destructive force of the wind. It is the only binding force on the plantless dunes. A moisture content of 1 per cent. holds the sand grains together only feebly, but at 2 per cent. the cohesive force is very manifest. Examples of this are best seen near Cape Woolamai, where the dunes are 100 feet high, and quite devoid of vegetation. Excavations along the sides of these show how moist they are.

Plants act in a twofold manner. The aerial portions are a direct obstacle in the path of the moving sand, and the particles are arrested. This action is important in the building of the dune. The roots do not assist in the building, but are resistant to the destructive action of the wind. On the lee side of the dune the sand comes to rest at an angle of 32 deg. to the horizontal. This value has been taken from measurements at Wilson's Promontory, Lakes Entrance, and Sydenham Inlet. This angle of rest is usually found only at the inner face of the first dune, which is sparsely covered with vegetation, since the rapid deposition of sand makes it difficult for plants to establish themselves.

On the outer face of the first dune the angle of inclination is very variable, being frequently higher than the angle of rest, due to the holding action of roots of *Spinifex hirsutus.* These roots are long and slender, and bear very short laterals. The combined action of these is to resist the destructive action of wind. Measurements of Spinifex-fixed dunes at Lakes Entrance gave an average value of 49 deg. for the outer face, while at Wilson's Promontory the outer face in many cases was almost vertical.

Composition.

It has already been remarked that a pioneer vegetation must be drawn from those families and genera inhabiting the nearby vegetated areas. In habitats so widely different, it is obvious that but few species could occur in both. It is true that some do, but they occupy but a minor place in the vegetation. The author prefers to call such forms "versatile wides" since their distribution is not controlled by any particular set of ecological conditions. On the sand dunes are found such accommodating forms as *Pelargonium australe* and *Acaena Sanguisorba*, but they are not conspicuous. The dune vegetation is very distinctive, and is formed of characteristically littoral species. There is a close relationship, although naturally a pioneer settlement is sparse as regards number of species present, with the adjacent heathland floor, which has been called Cheltenham flora (5). In fact, some of the heathland consists of old dunes (5). The reason why the dune flora, with the exception of *Leptospermum laevigatum,* remains close to the sea, and does not move inland, is probably due to the change in the soil conditions. The leaves of the dune vegetation are large (see Table VII.) compared with the heath vegetation.

The composition in so far as the larger Dicotyledons are concerned, is essentially Australian, the characteristic genera being found in other typical Australian associations.

In Table VI. are given the commonly occurring species found on the dunes. A feature of this association is that there are no dominants, for in each phase the members are of almost equal height.

TABLE VI.—SPECIES OCCURRING ON SAND DUNES IN VICTORIA.

I.—MONOCOTYLEDONAE.

Gramineae—Spinifex hirsutus (V.C.).
Festuca littoralis (C.).
Cyperaceae—Lepidosperma gladiatus (F.).
Scirpus nodosus (F.).

II.—DICOTYLEDONAE.

Archichlamydeae.

Proteaceae—Banksia integrifolia (V.C.).
Polygonaceae—Muehlenbeckia adpressa (F.).
Chenopodiaceae—Rhagodia baccata (C.).
Aizoaceae—Mesembrianthemum aequilaterale (C.).
Ranunculaceae—Clematis microphylla (C.).
Rosaceae—Acaena Sanguisorba (F.).
Leguminosae—Acacia Sophorae (V.C.).
Geraniaceae—Pelargonium australe (F.).
Myrtaceae—Leptospermum laevigatum (V.C.).

Metachlamydeae.

Epacridaceae—Leucopogon parviflorus (C.).
Apocynaceae—Alyxia buxifolia (C.).
Myoporaceae—Myoporum insulare (V.C.).
Goodeniaceae—Scaevola calendulacea (R.R.).
Compositae—Olearia axillaris (V.C.).
Helichrysum cinereum (V.C.).
Calocephalus Brownii (C.).
Senecio spathulatus (C.).

V.C. = very common; C. = common; F. = frequent; R.R. = rather rare.

It will be seen that the families and genera so conspicuous on the adjacent heath lands, Proteaceae (*Banksia*), Leguminosae (*Acacia*), Myrtaceae (*Leptospermum*), Epacridaceae (*Leucopogon*), Compositae (*Olearia*), are found here. However, no commonly occurring characteristic species, with the exception of *Leptospermum laevigatum,* is common to both associations. It has already been pointed out that species as *Acaena Sanguisorba,* which are very subordinate members, are found also in other widely differing associations. They are capable of existing under very diverse environments. Such species are capable of being Wides in the sense of Willis (11). There is a connexion, too, with the Fern Gully Association in the families Compositae (*Olearia*), Leguminosae (*Acacia*), Ranunculaceae (*Clematis*), and Apocynaceae. The last family is mostly tropical, but is represented here by two genera, each with one species.

The pioneers of this new land are therefore derived from the adjacent vegetation. However, since no species except one is common, it may be taken that a long time has elapsed since they first arose. Their lack of spread is an argument against Willis's (11) Theory of Age and Area, in so far as time only is concerned. The theory is true in a general way, but the confining of a species to a particular area is not necessarily because it is new born, nor because of any physical barrier to its spread, but possibly because of the dissimilarity of ecological conditions. The characteristic dune species are ecologically spot-bound.

One family of interest is Myoporaceae, which has a great development in the Mallee. Very frequently *Casuarina stricta* is found on the innermost dunes, and this tree is also a versatile wide.

Succession.

It has already been noted that the vegetation on this narrow strip along the coast, from outermost to innermost dune, is very diverse, and in other areas would be divided into separate associations, but here the same set of factors, wind and sand, operate, modified by the interference of the pioneers. The steady arrest of the moving sand is associated with a number of other changes, and the sequence of these changes is known as Succession.

The outermost dune is usually sparingly covered with *Spinifex,* with which a few other plants are sparsely associated. In Pl. IX., C, is shown an outermost dune at Lakes Entrance, where *Spinifex hirsutus* is the chief species, but both *Senecio spathulatus* and *Calocephalus Brownii* are also sparingly present. Occasionally *Festuca littoralis* is met with. The binding action of the roots and rhizomes, and the accumulative action of the leaves steadily bring about more stable conditions. At Lakes Entrance, *Spinifex* is abundant on the outer part of the second dune, but here low, extensive, prostrate masses of the so-called *Acacia Sophorae* effectively protect the soil (Pl. VIII. C.). This Acacia is in all probability but a biotype of *Acacia longifolia* which occurs in the rearmost dunes. It may, however, be merely a habitat form of the latter. At Lakes Entrance probably the most extreme forms of it occur. The phyllodes are exceedingly thick (Fig. 3) and broad. This *Acacia* sends out widely spreading horizontal roots, which are close to the surface, and may be exposed by the wind. On the underside of these, secondary roots occur, which grow downwards. On these, nodules of *Bacillus radicicola* are abundantly produced. In this spreading mass of the *Acacia,* plants of other species, particularly *Olearia axillaris,* are found. The *Acacia* marks the end of the *Spinifex* phase (Pl. VIII. C.) and the commencement of the scrub phase, which is composed, in addition to the two species just mentioned, of *Helichrysum cinereum* and *Scaevola calendulacea,* which may also form extensive prostrate masses. With these may be associated smaller plants as *Acaena Sanguisorba, Pelargonium australe,* and *Mesembrianthemum æquilaterale.* These latter are infrequent, and never affect the physiognomy. There is a marked difference here between these two successive stages. The vegetation is higher, and covers considerably more than half the surface of the soil. In the scale suggested by Braun Blanquet (1) the plant cover (Deckungsgrad), on the outermost dune being less than 5 per cent. has a numerical value of 1, while in the shrub or second phase (Pl. VIII., D) the area of soil covered is between 50 per cent. and 75 per cent., and to this the value 4 is given. The change is very abrupt, as can be seen in Pl. VIII., C. On the innermost dune (Pl. VIII., B) the degree of soil covering is complete, and this has the numerical value of 5. In this last phase, shrubs are replaced by small trees, and associated with these are both lianes and parasites. The tree species are *Banksia integrifolia, Myoporum insulare, Leptospermum laevigatum*, and with these are associated the tall shrubs *Alyxia buxifolia* and

Phase I.	Phase II.	Phase III.
Senecio spathulatus.	*Acacia Sophorae.*	*Leptospermum laevigatum*
Calocephalus Brownii.	*Olearia axillaris.*	*Myoporum insulare*
Spinifex hirsutus.	*Helichrysum cinereum.*	*Banksia integrifolia*
Festuca littoralis.	*Scaevola calendulacea.*	*Alyxia buxifolia*
	Myoporum insulare.	*Leucopogon parviflorus*
	Banksia integrifolia.	*Clematis microphylla*
	Clematis microphylla.	
	Acaena Sanguisorba.	
	Pelargonium australe.	
	Spinifex hirsutus.	

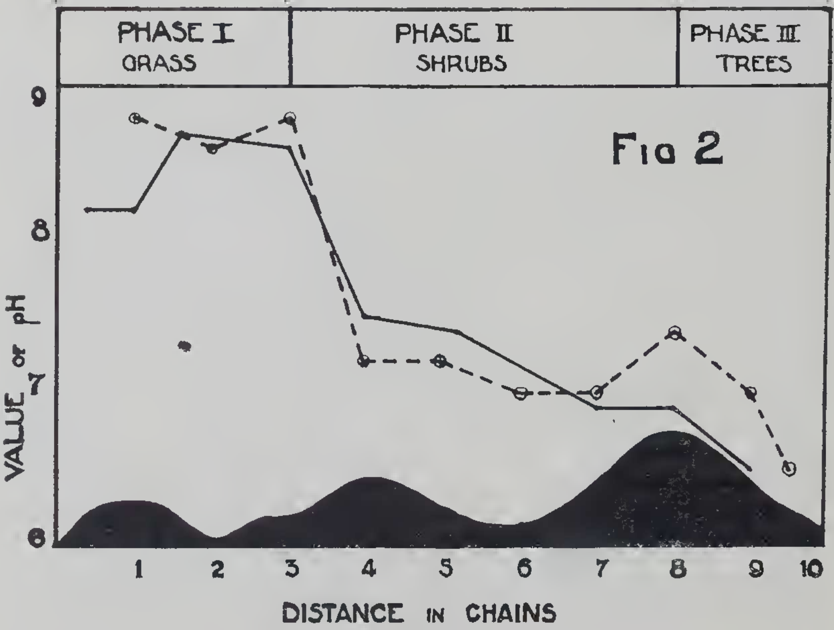


Fig. 2.—Variation in the soil acidity from front to rear of the sand dunes.

Leucopogon parviflorus. The degree of soil cover is so great—denser than any other local association, except possibly the Fern Gully—that there is an accumulation of raw humus. This is unusual in warm temperate climates. The dampness is shown by the presence of species of Bryophyta. The soil may be discoloured for several inches, due to the accumulation of plant debris. The slowness of decomposition of the leaves may be due to the thickness of the cuticle (Fig. 3). No such accumulation, however, occurs on the adjoining heathlands, for here the material is quickly decomposed.

The presence of the tree phase gives opportunity for other life forms to occur, such as lianes, but only one, *Clematis microphylla,* is commonly met with. Occasionally another liane, *Muehlenbeckia adpressa,* also occurs. In this phase phanerogamous parasites make their appearance, being represented by a species of Loranthaceae.

The succession above ground, life forms, species, height of phases, degree of soil cover, fixation of sand, accumulation of litter, is also associated with a succession as regards soil acidity. This is to be expected, since in the foremost dunes shell fragments occur, and in the innermost dunes plant remains are accumulating. In Fig. 2 are given two graphs of the pH values, ascertained by the Hellige Comparator, from front to rear of the dunes, one series of soil samples being taken at regular intervals of a chain, and the other being taken from front, top, and rear of each dune respectively.

Morphology.

The leaves of the dune plants are essentially xeromorphic (xeromorphy being defined as by Thoday (8)), but it cannot be contended on that account that the plants are xerophytic, since there is usually no deficiency of water for deeply penetrating roots. Although there is sufficient soil water, the strong winds provide a powerful desiccating force. Hence the xeromorphy must be ascribed to this cause. The xeromorphy extends right through the succession, those leaves occurring in the more favorable situation behind the third dune are just as xeromorphic. There are some truly mesomorphic leaves, as those of *Acaena Sanguisorba, Pelargonium australe,* and *Clematis microphylla,* but these plants occur in sheltered places, and are not exposed to the wind.

The xeromorphy of the leaves does not express itself in any particular direction, for we find that there is no uniformity as regards the leaf in (1) size, (2) structure, (3) cuticle, (4) disposition or number of stomata, (5) moisture content.

Size of Leaf.

Size is very variable, ranging from the leptophyll of *Calocephalus Brownii* to the microphyll of *Banksia integrifolia.* In Table VII. is given the percentage of leaf sizes according to Raunkaier (7) for the dunes at Lakes Entrance. The monocotyledons are excluded, as Raunkaier's system is not applicable to these.

TABLE VII.—LEAF SIZE CLASSES OF DUNE VEGETATION AT LAKES ENTRANCE.

	Per cent.
Leptophyll	20
Nanophyll	33
Microphyll	47

It is surprising to find so high a percentage of microphyllous leaves, for in adjacent heath flora only one microphyll is found. On the other hand, in the heath flora, leptophyllous leaves are abundant (5), while in the dune vegetation they form only 20 per cent., and these are all species of Compositae, confined to the first and second dunes.

STRUCTURE.

The leaf types, so far as the arrangement and development of tissues are concerned, may readily fall into three classes—normal, isobilateral, and succulent.

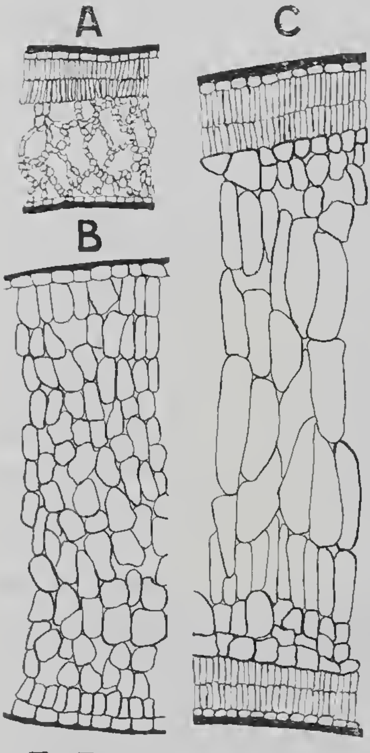


Fig 3.

FIG. 3.—Section of leaves of Dune Vegetation. (A) *Alyxia buxifolia*; (B) *Senecio spathulatus*; (C) *Acacia Sophorae* (section of leaf from exposed position).

(*a*) *Normal.*—The normal type (Fig. 3A) has palisade cells on the upper side, a well developed spongy mesophyll below, and stomata confined to the lower surface. These leaves are placed horizontally, and function as ordinary mesophyllous leaves. The spongy mesophyll is particularly well developed, and the air spaces are abundant. This type is represented by *Banksia integrifolia, Alyxia buxifolia*, and *Olearia axillaris.*

(*b*) *Isobilateral.*—The phyllode of *Acacia Sophorae* has almost identical structure with the true leaves of *Myoporum insulare* and *Leptospermum laevigatum* (Fig. 3, C). In these organs the palisade occurs on both surfaces, and stomata occur on both also. The association of stomata with palisade is an inversion of the normal structure. There is no spongy mesophyll, and the tissue between the outside layers of palisade is thin-walled and devoid of chlorophyll. This tissue is pith-like in character. The leaves of this type are not horizontal, but are more or less vertical. In *Acacia* the leaves are held strictly upright.

(*c*) *Succulent.*—There is a greater variety here than in the other two types, but the modifications are all in the direction of dispensing with normal cell arrangement and of ,conversion of all tissues to water storage. The family Aizoaceae is represented by *Mesembrianthemum aequilaterale* and *Tetragona implexicoma;* in the latter even the epidermal cells are converted into water vesicles. Also the family Chenopodiaceae, which contains many succulents, is represented here by *Rhagodia baccata.* Of more interest, however, is *Senecio spathulatus* (Fig. 3, B), which occurs on the outermost dune, and *Scaevola calendulacea.* In these two latter, palisade tissue is non-existent, and there is no normal spongy mesophyll. The cells are thin-walled, and air spaces are fairly plentiful. Stomata occur on both surfaces. Chlorophyll may occur right through the leaf, but it is not concentrated in particular layers as in the first two types.

Cuticle.

The xeromorphy expresses itself particularly in regard to the development of the cuticle. This reaches its greatest development in *Acacia Sophorae*, where it occurs on the exposed parts of the second dune. These measurements of the cuticles, given in Table VIII., are taken from leaves collected at Lakes Entrance. It is of interest to note that all of the species occurring in the shelter of the third dune have well-developed cuticles.

Table VIII.—Thickness of Cuticle of Leaves of Sand Dune Plants.

	Microns (μ)
Acacia Sophorae	18.6
Alyxia buxifolia	15.2
Olearia axillaris	15.0
Banksia integrifolia	13.6
Myoporum insulare	13.0
Leptospermum laevigatum	12.2
Senecio spathulatus	9.6
Spinifex hirsutus	8.0

Stomata.

Mostly the stomata are sunk beneath the level of the cuticle, and this fact, together with the thickness of the cuticle, may be regarded as protection against excessive transpiration. The number of stomata per sq. mm. is, on the whole, only moderate. A feature of the association is the number of plants that have stomata on both surfaces. Since the stomata are sunken, and since they do not abut on spongy mesophyll where diffusion readily takes place, and also since the leaves are thick, or very thick, stomata are probably necessary on both surfaces in order to fulfil the ordinary functions of a plant. To have stomata on both surfaces gives double the efficiency. However, it must be emphasized that as regards number of stomata per unit area, comparisons between an ordinary mesophytic dorsiventral leaf and a xeromorphic leaf, such as occur here, are of very little value, since other structures of the leaves are so widely different. The number of stomata per sq. mm. is given for the dune plants in Table IX.

Table IX.—Number of Stomata per sq. mm. on Leaves of Sand Dune Plants.

Leaf Type.	Species.	Average Number on Each Surface.
Normal	*Alyxia buxifolia*	152 — 0
	Acacia Sophorae	138 — 138
Isobilateral	*Leptospermum laevigatum* ..	122 — 58
	Myoporum insulare ..	69 — 69
Succulent	*Senecio spathulatus* ..	69 — 69
	Scaevola calendulacea ..	82 — 48

Further it may be remarked that the number of stomata per unit area cannot be ascertained from such plants as *Spinifex hirsutus,* where the stomata are set in grooves, nor from *Banksia integrifolia,* because the stomata are not uniformly distributed over the leaf, but are localized between broad sclerenchymatous strands. Where the veins are excessive, there cannot be any effective measure of the number of stomata per sq. mm., but some larger unit is needed. In other words the sq. mm. is too small a unit for leaves that have a great number of veins. It is of interest to note that *Acacia melanoxylon,* found in the Fern Gully, averages 307 stomata per sq. mm. on each surface of the phyllode.

Moisture Content.

It is natural to expect that sclerenchymatous leaves would necessarily contain a low amount of water. It has already been shown (5) that the moisture content of the heath plants, which are true xerophytes, is low. These leaves are generally xeromorphic and sclerenchymatous. If we consider similar leaves here, we find also a low average content of the leaves, namely, 163 per cent., calculated to the dry weight.

Leaves such as those of *Myoporum insulare,* which are xeromorphic and coriaceous, have a high moisture content, and such leaves might almost be classed as semi-succulent.

The true succulents—*Senecio spathulatus, Scaevola calendulacea,* and *Tetragona implexicoma,* have a very high moisture content.

In Table X. are given the moisture contents, calculated to dry weight, of typical dune plants.

TABLE X.—MOISTURE CONTENT OF THE LEAVES OF DUNE PLANTS GIVEN AS A PERCENTAGE OF DRY WEIGHT.

Helichrysum cinereum	118
Leptospermum laevigatum	121
Banksia integrifolia	129
Alyxia buxifolia	165
Spinifex hirsutus	184
Acacia Sophorae	275
Myoporum insulare	408
Scaevola calendulacea	635
Senecio spathulatus	683
Rhagodia baccata	756
Tetragonia implexicoma	1,040
Mesembrianthemum aequilaterale	1,338

Adaptation to Environment.

Warming (10) has given certain adaptations of plants growing on sand, and these in part are the case here. *Spinifex hirsutus* has long runners (Pl. IX. B.), in cases up to 20 feet, but normally the moving sand does not permit unrestricted development. These runners are facultative rhizomes, for when buried the runner functions as a rhizome, and sends up shoots. *Acacia Sophorae,* which is the immediate successor to *Spinifex hirsutus,* has also prostrate shoots which root at intervals. This is an unusual character for the genus *Acacia.* This habit enables the *Acacia* to form large masses (Pl. VIII. C.).

Another adaptation given by Warming is that of tufted habit, which is exemplified by *Senecio spathulatus.*

Hairiness is not an outstanding character, for it occurs on but a few plants. Glabrousness is more common. *Senecio spathulatus* is quite glabrous, and this occurs (Pl. IX. C.) side by side with the very hirsute *Spinifex hirsutus.* The leaves of the shrubby Composites are hairy underneath, as are also those of *Banksia integrifolia.* The cushion plant, *Calocephalus Brownii,* exhibits the extreme case of hairiness.

Succulence occurs only to a minor extent. The extremely succulent members of Aizoaceae are not very frequent. Instead of succulence, sclerophylly is more often the case both in the foremost and last dunes. Succulence and sclerophylly are found side by side in *Senecio spathulatus* and *Spinifex hirsutus.*

As a possibly important factor in the vegetation, light might be considered. There is a powerful reflection from the glistening white sand, particularly on the first dune and the outerside of the second dune. It cannot be said, however, that there is any particular adaptation against it. As soon as vegetation covers the sand, this factor ceases to be of importance, yet the morphological characters of the vegetation persist.

The outstanding example of adaptation to environment is to be found in *Spinifex hirsutus.* Its whole organization is a marked series of adaptations. This plant grows on the exposed outer dune, and its life is spent in one long continuous struggle with adverse conditions. It is the ultimate victor in the suppression of the destructive forces, but at times it suffers defeat and destruction.

In its habit of rooting, each node sending down a few long sparsely branched roots, it not only obtains a constant supply of moisture, but (Pl. IX. A.) binds the sand together against erosion by wind. These roots, even when dead, still have binding power. The runners when buried send up shoots to the new surface, and shoots and rhizome combined assist the roots in sand binding. Another adaptation is to be found in the fact that the stomata occur in grooves on the upper surface of the leaf which is mostly inrolled. In addition to the hairiness, there is a cuticle. When the leaf is inrolled the stomata are no longer exposed to the air, and thus transpiration is restricted. In addition, cuticle and hairy covering prevent cuticular transpiration. The plants are dioecious, and therefore must be wind-pollinated. The distribution of the seed (Pl. IX. D.) is again wind-controlled. The inflorescence breaks off, and is rolled by the wind, dropping the seed until it finally is arrested by the shrub succession. These spherical inflorescences are extremely light and easily moved. In germination there is a final adaptation. In seeds which have a coleoptile, the depth of soil through which the seedling can emerge is limited by the length of the coleoptile. In general the coleoptile is a very short organ, and limits the depth to which grass seed may be sown. Once the coleoptile ceases growth in length, the first leaf emerges, and leaves are very poor instruments for getting through the soil. The percentage of germination very rapidly falls when the seed is sown deeper than the length of the coleoptile. In *Spinifex hirsutus,* however, where there is the constant danger of the seed being buried deeper than the length of the coleoptile, there occurs a hypocotyl which can carry the coleoptile high up towards the surface of the sand. From seed to tip of coleoptile, 5 inches have been measured.

Generally speaking, there cannot be said to be any one constant adaptation in this association except prevention of water loss due to the constant wind. The modification of leaf structure, whether sclerophyll or succulent, is most probably connected with wind action. Where there is water supply at the root, xeromorphy is not a matter of course, no matter how powerful the condition for transpiration and evaporation may be.

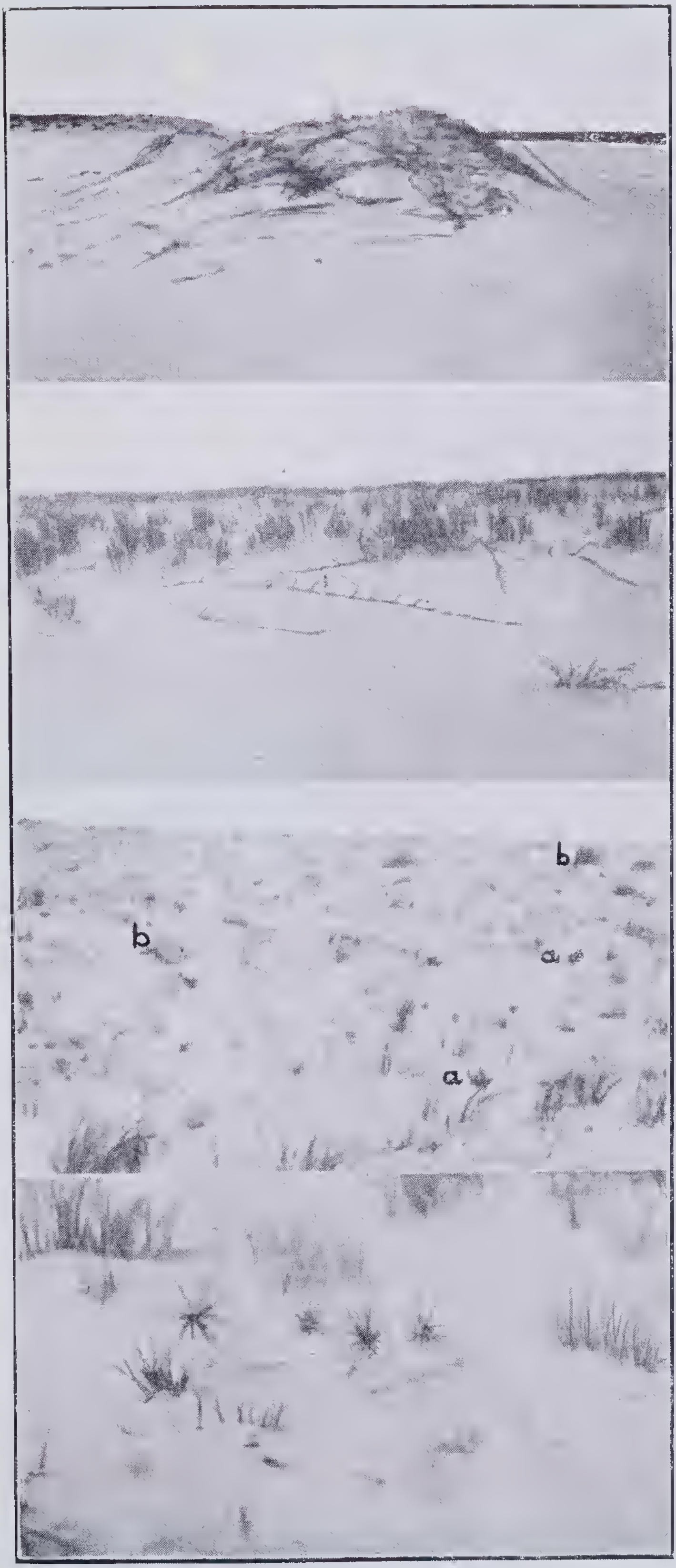
A

B

C

D

[Page 153.] Vegetation of Sand Dunes.



A

B

C

D

[Page 155.]

Vegetation of Sand Dunes.

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Explanation of Plates VIII. and IX.

Plate VIII.

A.—Second Dune showing the junction of Phase I. (Grass) and Phase II. (Shrubs). Photograph taken from top of First Dune looking towards the Third Dune. *Banksia integrifolia* on upper left.

B.—Third Phase (Trees) of Dune Vegetation. Photo taken from top of Third Dune seen in A.

C.—Prostrate masses of Acacia Sophorae at junction of Phases I. and II.

D.—Shrub phase. Photo taken from rear of Second Dune looking towards the Third Dune.

Plate IX.

A.—*Spinifex hirsutus* protecting an isolated Dune against denudation.

B.—Runners of *Spinifex hirsutus* on top of First Dune advancing seawards.

C.—Top of First Dune. Vegetation mainly *Spinifex hirsutus*, but at (*a*) are seen plants of *Senecio spathulatus* and at (*b*) specimens of the Cushion Plant, *Calocephalus Brownii*.

D.—Inflorescences of *Spinifex hirsutus*.